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Hind limb of the *Nacholapithecus kerioi* holotype and implications for its positional behavior (**revised**)

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Abstract

We present the final description of the hind limb elements of the *Nacholapithecus kerioi* holotype (KNM-BG 35250) from the middle Miocene of Kenya. Previously, it has been noted that the postcranial (i.e., the phalanges, spine, and shoulder girdle) anatomy of *N. kerioi* shows greater affinity to other early/middle Miocene African hominoids, collectively called "non-specialized pronograde arboreal quadrupeds", than to extant hominoids. This was also the case for the hind limb. However, *N. kerioi* exhibits a unique combination of postcranial characters that distinguish this species from other early/middle Miocene African hominoids. The femoral neck has a high angle, but is relatively short, though the adaptive meaning is not readily understood. In the distal femur, the shape of the patellar surface and symmetry of the femoral condylar widths suggest that the knee was not typically abducted but assumed more variable movements and/or postures. Whereas the morphologies of the talocrural and intertarsal joints are generally similar to those of the other fossil hominoids, the tibial malleolus is extremely thick and asymmetry of the talar trochlea groove is more emphasized due to a more prominent lateral trochlear rim than in *Proconsul* and other African fossil hominoids. The distal foot segment is more elongated. The (non-hallucal) metatarsals appear relatively gracile due to the elongation. The proximal joints of these metatarsals are, nonetheless, large. Ligamentous attachments of the tarsal/metatarsal bones are generally well developed. The distal tarsal row, which is represented only by the medial cuneiform, though, is extremely large for the presumed body mass. In terms of function, the femur, ankle, and tarsal joints are interpreted behaviorally to represent a slow-moving arboreal quadruped. However, the foot of *N. kerioi* appears to be more specialized for inverted grasping and subvertical support use. All of these foot features are suggestive of a greater role for antipronograde activities in *N. kerioi* relative to other Miocene "pronograde arboreal quadrupeds".

Keywords: Miocene, hominoids, positional behavior, fossils, functional adaptation

Introduction

This article provides the final description of the hind limb bones of the KNM-BG 35250 *Nacholapithecus kerioi* skeleton and discusses the functional adaptations of the species in light of these remains. *N. kerioi* is a baboon-sized hominoid known from the middle Miocene Aka Aithepus Formation (15 Ma) in Kenya (Ishida et al., 1999). Compared to early Miocene hominoids, which are best represented by fossils of *Proconsul* (Napier and Davis, 1959; Walker and Pickford, 1983; Walker and Teaford, 1988), postcranial anatomy of middle Miocene hominoids in East Africa was relatively unclear. However, in the late 1990s, a few partial skeletons of middle Miocene hominoids were discovered, and understanding of the morphology of these species was improved (Nakatsukasa et al., 1998, 2007a; Ward et al., 1999, Ishida et al., 2004). KNM-BG 35250 from Nachola (Nakatsukasa et al., 1998; Ishida et al., 2004) and KNM-TH 28860 from Tugen Hills (Ward et al., 1999) were important discoveries that helped clarify the diversity of middle Miocene hominoids in East Africa. KNM-BG 35250 was preliminarily described after its discovery (Nakatsukasa et al., 1998; Ishida et al., 2004). Since then, full descriptions of the phalanges (Nakatsukasa et al., 2003), shoulder girdle (Senut et al., 2004) and vertebral column (Nakatsukasa et al., 2007b) have been completed.

Contemporaneous to *N. kerioi* are *Equatorius africanus*, *Kenyapithecus wickeri* and *K. kizilli* (McCrossin, 1994; McCrossin and Benefit, 1997; Ward and Duren, 2002; Kelley et al., 2008; Harrison, 2010) and somewhat older is *Afropithecus turkanensis* (Leakey et al., 1988). Although the higher taxonomy of these hominoids is debated (Begun, 2002, 2007; Harrison, 2002, 2010; Ward and Duren, 2002), there is a general consensus that these species share derived traits such as thicker enamel and robust jaws and (at least many of them) form a clade exclusive of earlier hominoids in East Africa such as *Proconsul*. Postcranially, these groups show derived conditions relative to *Proconsul* in terms of increased orthograde (Nakatsukasa and Kunimatsu, 2009) or terrestriality (McCrossin, 1994; McCrossin and Benefit, 1997; McCrossin et al., 1998), while *Afropithecus* generally resembles *Proconsul* (Ward, 1998). The evolutionary scheme of hominoids

through the early and middle Miocene is vague and there is no consensus how to relate these African taxa to later extinct and extant hominoids (Nakatsukasa and Kanimatsu, 2009). This article is dedicated to the functional anatomy of the hind limb and does not deal with phylogeny since craniodental morphology provides more reliable estimates of such relationships. Viewed within this context, it remains important to reconstruct postcranial morphology, specifically hind limb functional anatomy, within *N. kerioi* to better understand the diversity of locomotor patterns in middle Miocene hominoids

The first study of hind limb functional anatomy of *N. kerioi* was done by Rose et al. (1996), which described 13 isolated hind limb specimens of *N. kerioi* (seven proximal femoral fragments, one patella, two distal fibula, one talus, one calcaneus, and one hallucal metatarsal; phalanges are not counted here) together with other postcranial elements in the 1980s collection. According to Rose et al. (1996), the working position of the hind limb in *N. kerioi* was partial flexion and external rotation and the talocrural joint could bear load effectively in the partial flexion and external rotation. While this functional adaptation was best matched with *Proconsul*, the authors noted some features (e.g., enlarged medial process of the calcaneal tuberosity) that suggest a greater role of orthograde climbing in *N. kerioi*. Later studies of the shoulder girdle, phalanges, and vertebral column of KNM-BG 35250 (Nakatsukasa et al., 2003; Senut et al., 2004; Nakatsukasa et al., 2007b) generally support these earlier conclusions. The present study aims to retest the interpretation by Rose et al. (1996) using new materials and to unveil characters that were unknown in the previously available specimens. We compare the hind limb elements of *N. kerioi* with those of early and middle Miocene hominoids from East Africa (*Proconsul* spp., *Ugandapithecus major*, *Morotopithecus bishopi*, *Afropithecus turkanensis*, *Equatorius africanus*). There are numerous studies of the hind limb functional morphology of these fossil hominoids and the basal catarrhine (Le Gros Clark and Leakey 1951; Zapfe 1960; McHenry and Corruccini 1976; Conroy and Rose 1983; Walker and Pickford 1983; Langdon 1986; Rose 1986, 1993; Rose et al., 1992, 1996; Gebo and Simons 1987; Leakey et al., 1988; Leakey and Walker 1997; Ruff et al., 1989; Ward et al., 1993; McCrossin

1994; McCrossin and Benefit 1997; McCrossin et al. 1998; Benefit and McCrossin 1995; Rafferty et al., 1995; Gebo et al., 1997; Walker 1997; Ankel-Simons et al. 1998; Gommery et al., 1998, 2002; Ward 1998; MacLatchy et al., 2000; Madar et al., 2002). This comparison will clarify different/similar functional anatomies of the hind limb in these African Miocene hominoids.

Material and Methods

Hind limb elements of KNM-BG 35250 are listed in Table 1. Since the pedal phalanges have been fully described elsewhere (Nakatsukasa et al., 2003), these elements are excluded from the list. Original specimens of *N. kerioi* and other comparative hominoids were studied in the National Museums of Kenya and the Uganda Museum. Only *E. africanus* specimens housed at the Natural History Museum (London) were examined using high quality casts. Comparative extant primate samples were studied in the Osteology Department, the National Museums of Kenya, Powell-Cotton Museum, and the Anthropological Institute and Museum, University of Zurich. Since most elements of KNM-BG 35250 are subjected to deformation, metric comparison was limited. Linear measurements were taken by using sliding calipers accurate to one tenth of the nearest millimeter. Angles were measure on digital photographs that were taken with settings to reduce parallax.

Table 1

Repeatedly used terms of anatomical orientation are abbreviated as follows: a-p = anteroposterior/-ly; m-l = mediolateral/-ly; s-i = superioinferior/-ly; p-d = proximodistal/-ly; d-v = dorsoventral/-ly; d-p = dorsoplantar/-ly.

Ischium

Description

The left ischial specimen (KNM-BG 35250G: Figure 1a) preserves the caudal half of the lunate surface

and a short part of the ramus (18 mm long from the acetabulum). A fracture runs obliquely crossing the caudal part of the acetabulum to the dorsal border of the ischial ramus around 1 cm below the ischial spine. The cross section of the ramus is rather flat (8.8 mm thick and 22.6 mm wide at the break) probably due to postmortem d-v compression. From the acetabulum, neither diameter nor depth can be obtained reliably. The maximum width of the preserved part of the lunate surface is ca. 14 mm. The ischial spine is prominent. It would have been about the level of the caudal acetabular border if the ischium were not subjected the fracture. Caudal to the spine is a well-defined marking by *mm. gemelli* and the tendon of *m. obturator internus*.

Figure 1

The right ischium (KNM-BG 35250Y: Figure 1b) is rather fragmentary. It is a ca. 4 cm long piece, preserving the caudal part of the lunate surface and a shorter length of the ischial ramus. No additional information is added.

Comparative Remarks

Where comparison is possible, the ischium of *N. kerioi* generally resembles that of *Proconsul* spp. Although it differs from that of *P. nyanzae* regarding a more cranial position of the ischial spine (see Ward et al., 1993), there is variability regarding this feature in *P. heseloni*. While it is caudally positioned in the KNM-KPS 8 individual, it is close to the caudal acetabulum rim in KNM-KPS 3. Although it was suggested that the lower position of the ischial spine was related to a greater development of tail muscles (McCrossin, 1994), it is now known that *P. heseloni* did not have a tail (Ward et al., 1991; Nakatsukasa et al., 2004). Therefore, the functional significance of this character remains an open question.

Femur

Description

Both the right and left femora consist of separated proximal and distal end pieces. The proximal piece of

the right femur (KNM-BG 35250A) shows several important characters, though postmortem cracking and deformation is apparent (Figure 2b). The left proximal piece (KNM-BG 35250D) lacks the head and most of the neck, and is crushed in the a-p direction (Figure 2c). However, KNM-BG 35250D preserves the greater and lesser trochanters, which are broken in KNM-BG 35250A. Thus, the morphology of the proximal femur is principally described based on the right piece and is supplemented by the left one. The distal piece of the right femur (KNM-BG 35250B) is crushed in the m-l direction and the left one (KNM-BG 35250J) in the a-p direction (Figure 3). The morphology of the medial and lateral epicondyles was observed in the former specimen and that of the condylar and patellar surfaces in the latter.

Figures 2, 3

The head of KNM-BG 35250A displays strong anteversion. In superior view (Figure 2a), the center of the head is weakly displaced anteriorly relative to the neck axis. Furthermore, the head is strongly rotated to face anteromedially. Although a moderate head displacement is not unusual in extant anthropoids, such an emphasized rotation is anomalous and should be regarded as deformation. Both the s-i and a-p diameters of the head are 22.1 mm. Relative to the neck thickness the head is large but less so than in extant apes (Table 2), suggesting a moderately wide range of movement at the hips joint (Ruff et al., 1989; Ward et al., 1993; MacLatchy et al., 2000). The articular surface of the head is preserved except the posterior margin. The articular surface is extensive and mushrooms over the neck except the abraded posterosuperior part (the articular border is indicated by an arrow in Figure 2d). In superior view, the articular surface depth (measured from the line passing through the anterosupeior and posterosuperior margin in Figure 2a) is 73 % of the head diameter. The fovea is oblong along the a-p axis (6.1 mm a-p, 3.4 mm s-i) and situated posteroinferiorly. The head extends proximally 9 mm above the most inferior level of the superior border of the neck. By matching this specimen with the left counterpart (Figure 2d and e), it is estimated that the superior surface of the head was 1.5 mm above the tip of the greater trochanter (Table 2).

Table 2

The neck-shaft angle is high (140°). This angle is comparable to that in gibbons and spider monkeys

(Rose et al., 1992; MacLatchy et al., 2000). The trochanteric crest is collapsed and closes the trochanteric fossa (Figure 2d). Although this damage precludes an accurate measurement of neck length, the neck is apparently short (Figure 2b). The cross section of the neck is moderately compressed in the a-p direction (16.2 mm s-i and 11.8 mm a-p). It is more expanded in the a-p direction in extant apes (Table 2). A large *crista trochanterica* is observed on the posterior aspect of the neck (arrows in Figure 2e) similar to *Proconsul* and *Morotopithecus* (MacLatchy et al., 2000).

The lateral side of the greater trochanter bears a protuberant insertion of *m. gluteus minimus*. The gluteal tuberosity is positioned at a relatively proximal level so that the gap between it and the insertion of *m. gluteus minimus* is narrow. The lesser trochanter of KNM-BG 35250D is wide s-i (16.7 mm at its base). It projects medially with weak retroflexion.

In KNM-BG 35250A, the anteromedial cortex of the shaft is cracked and widely collapsed into the medullary cavity. However, plastic deformation of the cortex seems weak. Approximate m-l diameter of the mid-shaft is 17.4 mm, which is taken at the most inferior level of the preserved cortex.

In the distal femur (KNM-BG 35250J), the patellar surface is square-shaped rather than trapezoidal in anterior view (Figure 3a arrows). The surface is wide (22.7 mm) compared with similar-sized cercopithecids (see Madar et al., 2002), which suggests an emphasis on knee rotation (Ward et al., 1995). The femoral condyles are symmetrical in width on the posterior aspect (Figure 3b). The medial and lateral condylar widths are 16.1 and 15.9 mm, respectively. If the postmortem a-p compression occurred evenly on the femoral condyles, then this symmetry should be the original condition. On the lateral epicondyle of KNM-BG 35250B (Figure 3c), there is a large, deep and round fovea for the lateral collateral ligament (lc). Distoposteriorly, there is a deep oblong depression for the tendon of *m. popliteus* (po). On the medial epicondyle (Figure 3d), there is a deep fovea for the medial collateral ligament (mc). The origin of *m. popliteus* is fairly developed but not groove-like as in *Morotopithecus bishopi* (MacLatchy et al., 2000).

Comparative Remarks

The previously described proximal femora (Rose et al., 1996) exhibit a close morphological affinity to these new specimens but are more fragmentary. Newly recognized characters are as follows: Head projection beyond the greater trochanter, wide articular cover of the head, moderately enlarged head relative to neck diameters, and high neck shaft angle. Characters of the distal femur are all new reports.

While the femur of *N. kerioi* generally resembles that of *Proconsul*, it differs from the latter in a higher neck angle, shorter neck, somewhat better developed posterior bar of the trochanteric fossa, more medially directed lesser trochanter, more proximally located gluteal tuberosity, and square-shaped patellar surface (rather than trapezoid), although intra-specific variability in these features should also be considered (Rose et al., 1996; this study; see Ward et al., 1993 for the *Proconsul* femoral features). These features, except the orientation of the lesser trochanter, distinguish *N. kerioi* from *Ugandapithecus major* (Gommery et al., 1998, 2002). The femur of *N. kerioi* remarkably differs from that of *M. bishopi*. In fact, *M. bishopi* is distinct among the African Miocene hominoids whose femoral morphology is known in its small femoral head relative to the neck (Table 2) and the absence of the anterior displacement of the head (MacLatchy et al., 2000). *N. kerioi* further differs from *M. bishopi* in the developed posterior trochanteric bar, better-developed gluteal ridge, stronger projection of the *m. gluteus minimus* insertion, less rounded neck cross-section and more symmetric femoral condyles (see MacLatchy et al., 2000). Despite of these differences, they are similar in showing the short and highly angled neck and medially projecting, proximally positioned lesser trochanter and (possibly) rectangular patellar surface. *N. kerioi* resembles *E. africanus* in the morphology of the proximal femur (Rose et al., 1996) and a square-shaped patellar surface [see McCrossin (1994)]. The femur of *E. africanus* is long and slender, and lacks marked m-l expansion (Le Gros Clark and Leakey, 1951; Ruff et al., 1989; McCrossin, 1994). Although the femur of *N. kerioi* seems to lack marked shaft m-l expansion, it is uncertain if the shaft is slender like *E.*

africanus. *N. kerioi* differs from *Sivapithecus* in a more emphasized platymery and m-l asymmetry of the distal femur in the latter (Madar et al., 2002).

Rose et al. (1996) interpreted that features of the proximal femur in *N. kerioi* are related to well-developed lesser and greater gluteal muscles and that the lesser gluteal muscles functioned as rotators as well as extensors during arboreal quadrupedalism and climbing. While engaging in these activities, the thigh must experience partial external rotation with the knee being partially flexed and pointing laterally. Newly recovered characters such as the wide articular coverage of the head, moderate expansion of the head and the high projection of the head concur with their interpretation. However, it is not readily explained why a relatively short neck is observed, which would sacrifice hip joint mobility. This is a conundrum that is also known in *M. bishopi*. To ensure a wide range of hip joint motion, a high neck angle should be essential for a short neck (MacLatchy et al., 2000).

The distal joint morphology complicates such a straightforward functional interpretation. An asymmetrically wider medial condyle is suggestive of emphasized loading of the medial side of the knee (Rafferty and Ruff, 1994; Mader et al., 2002). Thus, condylar width asymmetry in primates has been interpreted as an emphasis of thigh abduction in relation to arboreal quadrupedalism and/or climbing (Tardieu, 1981; Jungers and Susman, 1984; Fleagle, 1977; Fleagle and Meldrum, 1988; MacLatchy et al., 2000; Mader et al., 2002). If the knee of *N. kerioi* experienced habitual abduction, then condylar width asymmetry would have been accentuated similarly to *Proconsul* and *M. bishopi* (Figure 3e, Table 2). However, this is not the case.

The patellar surface morphology poses a similar question. A trapezoidal patellar surface with a proximally extended lateral side suggests that the contraction of the *vastus lateralis* was proportionally greater (Fleagle and Meldrum, 1988) and concerts with a flexed and abducted knee, a posture suitable for a medium-sized mammal to keep balance above a branch. While this is the case for in *P. nyanzae* (Figure 3e), the patellar

surface in *N. kerioi* is square-shaped. To our knowledge, there is no living large-sized primate that shows *N. kerioi*-like knee morphology. Though admittedly speculative, these differences may reflect that the knee joint took more various positions compared to *Proconsul*.

Patella

Description

The proximal half of the right patella (KNM-BG 35250Z) is preserved (Figure 4). The maximum m-l width is 22.6 mm, probably being 1 to 2 mm less than the true maximum width. The maximum a-p thickness is 9.8 mm. The articular surface is broad and weakly convex m-l. The proximolateral border of the superior surface forms an osteophyte projecting proximally.

Comparative Remarks

Due to the fragmentary nature, KNM-BG 35250Z adds little to knowledge already obtained from a previously collected specimen (KNM-BG 15535) (Rose et al., 1996). The m-l width of KNM-BG 35250Z is approximately 1.2 times of KNM-BG 15535, suggesting that the latter is a female specimen. Important features of *N. kerioi* patella are m-l wideness, a-p shallowness, and a shallow saddle-type articular surface, which permits conjunct/adjunct rotations around the a-p axis (Rose et al., 1996). This form is common with *P. heseloni* and *E. africanus* (McCrossin, 1994; Ward et al., 1995; Rose et al., 1996) and likely represents the primitive state for hominoids (Ward et al., 1995) or catarrhines (Rose et al., 1996).

Figure 4

Tibia

Description

The left tibia consists of three distinct pieces: 94 mm long proximal part with epiphysis (KNM-BG

Figure 5

35250E), 107 mm long shaft (KNM-BG 35250AF), and 30 mm long distal epiphysis (KNM-BG 35250H) (Figure 5a). The right tibia consists of 57 mm long proximal (KNM-BG 35250AE) and 27 mm long distal epiphyses (KNM-BG 35250L) (Figure 5h, e). All of these specimens were subjected to plastic deformation and cracking. Due to better preservation, the description is mainly provided on the left tibia for the proximal to middle section and on the right for the distal section.

KNM-BG 35250E is subjected to m-l compression. The medial plateau of the proximal surface is displaced posteriorly and the lateral plateau anteriorly (Figure 5c). The medial plateau is hemi-circular and shallowly concave. The a-p length is 26.6 mm. The lateral plateau is ovoid and 23.3 mm along its long axis. It is concave in the m-l direction and slightly convex in the a-p direction. The tubercles of the intercondylar eminence are abraded. The lateral condyle is thick and the s-i height measures 11.7 mm at the center of the fibular facet. The fibular facet is flat and faces distally (Figure 5a). It is 12.2 mm in length and 4.8 mm in width. A moderately wide tibial tuberosity (10.4 mm) is located 10 mm below the anterior border of the proximal surface.

Although the shaft piece (KNM-BG 35250AF) does not join with the proximal and distal piece, the shape of its proximal break suggests that only a short part is missing between it and KNM-BG 35250E (Figure 5a). The lateral cortex is broadly collapsed into the medullary cavity and no useful shaft measurements can be taken. The composite length of KNM-BG 35250E, AF and H (measured excluding the medial malleolus) is 217 mm. Given that the BM of KNM-BG 35250 was 22 kg (Ishida et al., 2004), a great ape prediction model estimates 225 mm and a cercopithecoid model 231 mm (Jungers, 1984). Thus, it remains unclear which model fits better. A subadult female *P. heseloni* (KNM-KPS 3), with an estimated BM of 9.3 kg (Rafferty et al., 1995), has a 181 mm long tibia, which accords with an estimate based on the cercopithecoid model (179 mm) rather than the great ape model (198 mm).

The right distal tibia (KNM-BG 35250L) is subjected to postmortem m-l compression (Figure 5d-f). The

posterior cortex is partially collapsed and the groove for the tendon of *m. tibialis posterior* is broken. The fibular notch is wide and deep, forming an angle of 120° in distal view. Due to surface erosion and a remaining matrix layer, the articular surface of the synovial distal tibio-fibular joint cannot be defined, unlike previous specimens (Rose et al., 1996). The trochlear articular surface is 19.8 mm in the a-p length. The articular surface is widest (13.8 mm) anteriorly and narrowest (10.9 mm) at the bottom of the fibular notch (these measurements are affected by deformation). A well-defined median keel divides the articular surface into the lateral and medial portions. The keel is pronounced anteriorly and ends at the median beak on the anterior border of the distal tibia. The lateral portion is wider than the medial one, especially in the anterior portion. The most anterior part of the medial portion faces distoanteriorly (Figure 5d). This part would contact the trochlear articular extension on the neck of the talus (see below) in full dorsiflexion. The lateral and medial portions are well concave a-p and to a lesser extent m-l. Although the medial malleolus is not long, it is thick (Table 3). A thick malleolus is common in extant apes. The malleolar articular surface extends onto the anterior aspect of the malleolus, occupying the lateral half of the surface (Figure 5d), to form a large malleolar-talar cup complex (see below). In distal aspect, the attachment area of the deltoid ligament is widely excavated.

Table 3

Two other tibial specimens add little useful information. The right proximal piece (KNM-BG 35250AE) is smashed m-l (Figure 5h). The inter-condylar eminences are prominent, probably due to postmortem deformation. There is a deep pit on the medial side of the medial condyle, which is likely the insertion of *m. semimembranosus* (Figure 5h). The left distal epiphysis (KNM-BG 35250H) is strongly compressed a-p (Figure 5g).

Comparative Remarks

The distal tibia of *N. kerioi* generally resembles that of *Proconsul* (e.g., KNM-RU 1939 *P. nyanzae*;

Figure 5i, j). Although proximal tibial specimens are not many, a thick lateral condyle is also observed in *P. heseloni* (e.g., KNM-KPS 3). Features of the talocrural articular surface (salient median keel, distoanteriorly facing facet) provide joint stability in the close packed position (Conroy and Rose, 1983). The talocrural joint of these fossil apes lacks specialized mobility that living apes attain, and is more like that of cercopithecoids in this regard (Conroy and Rose, 1983). *N. kerioi* differs from *Proconsul* in the greater thickness of the medial malleolus. This trait is probably related to emphasized medial loading during inversion (DeSilva, 2009), and suggests a greater proportion of climbing in its total locomotor behavior. The very high value in *U. major* (Table 3) is probably size-related.

Fibula

Description

The left fibula is represented by two separate pieces: 92 mm long shaft fragment (KNM-BG 35250AH) and 76 mm long distal fragment (KNM-BG 35250F) (Figure 6a-c). The right fibula is represented by 111 mm long shaft (KNM-BG 35250AG) and 19 mm long distal fragment (KNM-BG 35250K) (Figure 6d-f).

Figure 6

Both of the shaft pieces are flat m-l throughout and have a sharp anterior border and a rounded posterior border. Medially, a 3-4 cm long interosseous border runs distally from the proximal break in both specimens. Thus, these specimens preserve almost identical parts, with the right one preserving distally greater amount of the shaft. The right shaft is free from plastic deformation. It is widest a-p 4 cm above the distal break (11.0 mm). Comparing it with a well-preserved fibula of *P. heseloni* (KPS-FB 5), this appears to correspond to the original maximum a-p diameter. At this level, the m-l diameter is 7.3 mm.

In the (left) distal fibula (KNM-BG 35250F) the anterior border of the shaft changes course laterally as it descends distally, and approaches the apex of the fibular malleolus (Figure 6c). This leaves a triangular subcutaneous area on the anterior aspect of the bone. Medially, the attachment site of the anterior inferior

tibiofibular ligament is prominent. The maleollus is long and projects distally and slightly laterally. The malleolar fossa is deep. The talar facet morphology is affected by postmortem a-p compression. However, it otherwise appears similar to that of previously reported specimens (Rose et al., 1996).

Comparative Remarks

The fibular shaft and distal joint features in *N. kerioi* are largely comparable with *Proconsul* and *A. turkanensis* (Walker and Pickford, 1983; Rose et al., 1996; Leakey et al., 1988; Walker, 1997; Ward 1998, Ward et al., 1993). Notable features are a flat but very robust shaft and large fibular maleollus. These characters are related to the development of *m. flexor hallucis longus* and ligamentous reinforcement of the talocrural joint, in relation to a strong hallucal grasp (Walker and Pickford, 1983; Rose et al., 1996).

Talus

Description

The left talus (KNM-BG 35250I) is well preserved (Figure 7), although some damages are noted. The lateral tubercle of the posterior talar body is broken off. The medial tubercle is dorsally displaced. The talar head is dorsoplantarly compressed being resulted in m-l expansion and flattening of the distoplantar surface. Cortical cracks on the middle and posterior articular surfaces of the talocalcanean joint suggest that these regions also suffered from postmortem compression.

Figure 7

The trochlea is 15.5 mm in anterior width and 15.2 mm at mid-width [measurements following Rose et al. (1996)]. The a-p length is 23.2 mm along the lateral trochlear rim. The trochlea is moderately long (or narrow): Width/length ratio [index 1 in Rose et al. (1996)] is 70.7%. It is only faintly wedged posteriorly [wedging index = 96.2%; index 3 in Rose et al. (1996)] with the medial and lateral trochlear rims virtually being parallel (Figure 7a). The trochlear groove is deep, and the lateral rim is much higher than the medial one.

Thus, the lateral slope of the trochlear groove is far wider than the medial slope (Figure 7e). Although the medial rim might be lowered by postmortem compression, the asymmetry of the distal tibial joint (Figure 5) indicates that the medial rim was originally lower than the lateral rim. In dorsal view, the lateral rim projects more distally than the medial rim. The medial rim runs distomedially and continues to the anterior border of a cup-shaped depression (malleolar cup) on the neck (Figure 7a). The malleolar cup is large. Lateral to the malleolar cup and beyond the medial trochlear rim is a wide depression, which is reciprocal for the median beak on the anterior border of the distal tibia.

The lateral surface of the trochlea is moderately tall. This surface is vertical except for the triangular-shape inferior part (Figure 7c). Posterior to the lateral articular surface is a deep pit for the posterior talofibular ligament. The trochlear height measured at the most distal level of the lateral rim is 12.8 mm. The trochlear height/length ratio (56.9 %) is common in anthropoids [index 2 in Rose et al. (1996)]. The medial tubercle of the posterior talar body is very large (Figure 7b) as seen in some atelines (*Alouatta*, *Lagothrix*). This tubercle guides the tendon of *m. flexor hallucis longus* medially and bears the attachment of the posterior tibiotalar ligament.

On the plantar aspect, the posterior surface of the talocalcaneal joint is 17.5 mm long along the long axis and concave to a degree common in extant non-hominoid catarrhines. Its anterior margin is beveled distoanteriorly, to contact with the calcaneal body in the close packed position. The *sulcus tali* is deep, and it was certainly deeper before the fractures of the posterior and middle calcaneal articular surfaces (Figure. 7b: st). Medial to the distal articular surface of the talocalcaneal surface is a deep pit for the talo-navicular ligament (tn).

The neck deviates medially, forming an angle of 144° with respect to the medial trochlear rim. The neck is moderately wide (13.8 mm at the narrowest part) [index 4 (Harrison, 1982) = 59.5 %]. The relative neck length [index 3 (Harrison, 1982)] is also intermediate (65.9 %). The head is very wide (18.3 mm) with the

relative width [index 5 (Harrison, 1982)] of 78.9 %. However, this is exaggerated by postmortem deformation.

The original size of the head is unknown.

Comparative Remarks

Previously, the talar morphology of *N. kerioi* was reported based on KNM-BG 15529, a weathered talar trochlea (Rose et al., 1996). The trochlea of KNM-BG 35250I generally resembles this specimen (Figure 8), except its d-p taller form. This difference resulted from postmortem deformation in KNM-BG 15529.

The talar morphology is generally homogenous in African Miocene apes (Harrison 1982; Conroy and Rose, 1983; Langdon, 1986) and *N. kerioi* is not exceptional. The trochlea is a subtly asymmetric trapezoid with weak posterior wedging, rather than the asymmetric quadrangle with strong posterior wedging observed in extant African apes (Ward, 1998). It is neither very long nor very wide (Rose et al., 1996). The trochlear groove is deep being similar to cercopithecoids, though differing from the shallow morphology as observed in extant African apes (Harrison 1982; Conroy and Rose 1983; Langdon 1986). The lateral rim is higher than the medial rim (Harrison 1982). Like cercopithecoids, the malleolar cup is well developed and a concave tibial stop is formed at the distal border of the trochlear groove (Le Gros Clark and Leakey, 1951; Harrison, 1982; Conroy and Rose, 1983; Ward et al., 1993). The neck orients medially, more than orangutan, platyrrhines and prosimians, but less than gorillas and humans (Harrison, 1982). Since these features are generally common among *Pliopithecus* and small-sized non-cercopithecoid catarrhines from the Miocene of Africa, these represent the primitive catarrhine condition (Conroy and Rose 1983; Langdon 1986; Rose 1993; Ward et al. 1993). In these fossil African apes, inversion of the talocrural joint is intermediate between extant cercopithecoids and great apes, and conjunct inversion and abduction occur during dorsiflexion like the cercopithecoid ankle (Conroy and Rose, 1983). The tibial stop in the distal trochlea, and the malleolar cup provides the joint with stability in full dorsiflexion, which might have been taken in the propulsive thrust

toward the end of the stance phase in quadrupedal walking and/or climbing. This basic foot structure is representative of extant monkeys and apes, and was certainly suitable for a wide range of generalized arboreal activities (Conroy and Rose, 1983).

However, there is some (relatively minor) variation among these fossil hominoids. In *N. kerioi*, the asymmetry of the trochlea groove is more emphasized than in *Proconsul* and other African fossil hominoids due to a more prominent lateral trochlear rim (Figure 8), which may be related to effective weight transfer during inversion. The medial tubercle of the posterior talar body is remarkably large, suggesting greater development of the long hallucal flexor, which must be associated with the unusually large size of the hallux (Nakatsukasa et al., 2003). The implication is that *N. kerioi* engaged in climbing or other antipronograde activities more frequently compared to *Proconsul*.

Figure 8

Calcaneus

Description

The distal segment of the right calcaneus (KNM-BG 35250O) is preserved (Figure 9). The proximal break crosses the calcaneal body obliquely from the posterior base of the *sustentaculum tali* to the distolateral corner of the posterior talar facet (PTF). The *sustentaculum tali* is intact. The margin of the cuboid facet is eroded with exception of the plantar medial part.

Figure 9

The maximum breadth of the body (Harrison, 1982) is 25.4 mm. Although the distal segment (distal from the anterior border of the PTF) appears somewhat short, this is an artifact of erosion on the cuboid facet. The middle talar facet (MTF) on the sustentaculum is continuous with the anterior talar facet (ATF) via a narrow articular band (isthmus). The breadth of the MTF is 6.8 mm and the combined MTF/ATF length is 19.6 mm. The relative width of the MTF is as low (34.7 %) as macaque and gibbon (index 7 in Rose, 1986). The MTF/ATF region is strongly curved in medial view (Figure 9b). Lateral to the articular isthmus is a

distinctively deep (>2 mm) pit for the interosseous talocalcaneal ligament (ITL). Under the sustentaculum, there is a quite deep groove for the tendon of *m. flexor hallucis longus*. This condition is accentuated by the lateral expansion of the distomedial planter tubercle, the site of origin for the short plantar ligament and most fibers of the spring ligament.

Comparative Remarks

KNM-BG 352500 differs from the previously described calcaneus (KNM-BG 17805; Rose et al., 1996) (Figure 9d, e) in the height of the distal body and the deep pit formation for the ITL. However, the shallowness of the distal calcaneal body in KNM-BG 17805 is attributed to postmortem deformation (see below). In KNM-BG 17805, the attachment of the ITL is a shallow depression.

There is additional calcaneal material from the KNM-BG 15532 specimen, which was collected in 1984 and never reported (Figure 9f). KNM-BG 15532 is a distal half of a small right calcaneus, missing the calcaneal tuberosity, *sustentaculum tali* and medial half of the cuboid facet. The middle and distal segment length (distal from the posterior border of the PTF) is 24.5 mm. This specimen is likely a small female or an immature male. It resembles KNM-BG 17805 in the morphology of the medial plantar process (only its anterior portion is preserved) and KNM-BG 352500 in general morphology except for a shallower groove for the tendon of *m. flexor hallucis longus* (probably, size-related) and the absence of a deep ITL pit. The PTF of KNM-BG 15532 is almost intact. It is oval in outline (12.3 mm long and 8.1 mm wide) with its long axis being modestly angulated proximomedially to distolaterally. The relative width of 65.9 % is moderate (Rose, 1986). The PTF is tightly curved along the long axis. The degree of the curvature is tightest at midpoint. The cuboid facet is broken dorsomedially. The peripheral (lateral and dorsal) part of the cuboid facet is fairly wide and flat resembling calcanei of extant African apes (Rose, 1986).

These features are generally common in other African fossil hominoid calcanei. The subtalar articulation

probably had a greater range of motion than in extant cercopithecids but received habitual loading in either inversion or eversion, without large weight-bearing in transitional position (Conroy and Rose, 1983; Harrison, 1982; Rose, 1986; Rose et al., 1996; Ward et al., 1993). A good development of the medial plantar process suggests well-developed intrinsic toe flexors, which would facilitate toe grasp even during foot dorsiflexion (Sarmiento, 1983; Rose et al., 1996).

However, a deep pit for the ITL attachment site observed in KNM-BG 35250O is rare in fossil apes and living catarrhines. In *Proconsul*, its morphology varies from a shallow depression to a rugose surface. *U. major* (KNM-SO 390) shows a somewhat similar pit, but much less deep. This site is merely a rugose surface in *Sivapithecus* (Rose, 1986). Although a deep pit is observed in only one out of the three *N. kerioi* calcanei, none of the other African Miocene ape calcanei (about 10) show a similar feature. More *N. kerioi* specimens are necessary to evaluate the frequency and expression of this trait.

Medial cuneiform

Description

The left medial cuneiform (KNM-BG 35250AI) is almost intact (Figure 10). The a-p length is 18.8 mm. The d-p length is 21.8 mm. The relative length (Harrison, 1982) is 86.2%. The m-l width is 10.5 mm. The margin of the proximal (= navicular) articular surface is partly abraded. It is elliptical (9.4 mm wide and ~12 mm long).

The hallucal metatarsal (MT1) articular surface is 18.6 mm high. It is reniform and well convex m-l (Figure 10b). The MT1 articular surface in *N. kerioi* is not a simple ellipse. Its main articular region is a bulged band which spirals on the medial and distal sides of the bone superomedially to inferodistally. However, along the plantar articular border, the peripheral region incurves dorsally (upward). Therefore, the plantar third of the whole articular surface takes seller form.

On the lateral side, there are proximal and distal facets for the intermediate cuneiform, and the MT2 facet.

The latter facet is continuous with the distal facet for the intermediate cuneiform.

Figure 10

Comparative Remarks

The medial cuneiform of *N. kerioi* is similar to that of *Proconsul* in overall shape. However, the prehallux articulation, which is present in *Proconsul*, is absent in *N. kerioi*. The prehallux participates in the medial cuneiform-MT1 joint medioplantarly. The presence of this bone is a primitive feature retained in platyrrhines and gibbons (Lewis, 1972; Conroy 1976; Harrison, 1982). When the MT1 is fully abducted on the medial cuneiform, a bare joint surface remains on the medioplantar part of the articular surface in *Proconsul*, which would serve for the prehallux (Figure 10f). There is no equivalent surface in *N. kerioi*. An absence of the prehallux is also evidenced from the MT1 morphology (see below). However, the occurrence and development of the prehallux are rather variable individually and ontogenetically, and its utility for functional and phylogenetic consideration is questioned (Wikander et al., 1986). The medial cuneiform in *N. kerioi* is unusually large for its body mass being approximately equal to that of *P. nyanzae* (Figure 10). The large size is unquestionably related to the large hallux.

Metatarsals

Five MT specimens are associated with KNM-BG 35250. Four of them preserve the proximal joint. The remaining specimen is a non-hallucal MT head with a short piece of the shaft and cannot be assigned to a particular ray.

KNM-BG 35250AJ is the right MT1. The head is missing along with the distal shaft (Figure 11a, b). The preserved length is 39 mm. The shaft is squashed d-p. [Note orientations are defined by the human standard anatomy and differ from those in articulated position (= in opposition) here.] Likewise, the epiphysis is

compressed d-p to a lesser degree (Figure 11c). Due to this compression, the proximal articular surface is lower d-p and more tightly curved than it would have been. The articular surface is reniform. There is no articular extension on the medial side of the bone, which would contact with the prehallux if it exists (see Figure 11d).

The MT1s of African Miocene apes are generally uniform. It is large and robust and the proximal joint ensures good abduction-adduction mobility (Harrison, 1982; Walker and Pickford, 1983; Ward et al., 1993). The sole exception is *E. africanus*, which is reported to have a reduced articular surface of the proximal joint and suggested to have had a limited range of abduction (McCrossin, 1994).

A 20 mm long proximal part of the left MT2 (KNM-BG 35250AK) is preserved (Figure 11e, f). The proximal articular surface measures 11.4 mm m-l and 12.9 mm d-p. On the lateral side of the shaft, there are articular surfaces for the lateral cuneiform and MT3. On the medial side, there is a large-rectangular articular surface for the medial cuneiform (8.8 mm high, 5.2 mm long). The broken end of the shaft is ovoid being 6.9 mm m-l and 9.1 mm d-p. This specimen is similar to that of *Proconsul*, particularly KNM-RU5872P. The size of the epiphysis is also equivalent (11.2 mm, 12.5 mm). However, the shaft is more slender compared with *P. nyanzae* (8.2 mm m-l and 10.2 mm d-p at the comparable level).

The left MT4 (KNM-BG 35250AL) is a 30 mm proximal part (Figure 11g, h) and is squashed m-l. The cortex of the shaft is cracked and collapsed into the medullary cavity. The epiphysis is also compressed and the articular surfaces for the MT3 are flattened. The lateral surface bears an extensive, concave articular surface for the MT5 (Figure 11g).

The left MT5 (KNM-BG 35250AM) is broken proximal to the head (Figure 11k, l). The preserved length is 62.4 mm. The proximal articular surface is triangular in shape, wide (10.2 mm in width and 7.3 mm in medial height), and well convex d-p, which suggests hyper-dorsiflexion capabilities (Figure 11k). On the medial side, there is a large crescent articular surface for the MT4. The dorsal horizontal part is long and faces

dorsomedially. The styloid process is obtuse, but projects proximolaterally, with the insertion of the *m. peroneus brevis* located far laterally. Proximomedially on the plantar side, there is a tubercle for the origin of *m. flexor digiti minimi brevis* (Figure 11l, arrow). Between this tubercle and the styloid process, there is a groove for *m. abductor digiti minimi*. The shaft is slender. The cross section is d-p long and elliptical. At approximately mid level, it is 5.0 mm m-l and 5.8 mm d-p. This specimen closely resembles KNM-RU 5872H *P. nyanzae* specimen (Figure 11m). The latter specimen is slightly larger in overall size and the shaft is more robust.

A 3.0 cm long distal end of a metapodial (KNM-BG 35250AN) of a lateral ray has also been collected (Figure 11i, j). The head is squashed m-l. Even if deformation is taken into account, the narrowness of the head bears a greater reminiscence of a MT rather than to a metacarpal [e.g., KNM-BG 17807; see Rose et al. (1996)]. Apart from the head proportion, its articular features are common with those of the metacarpal (which is also true for *P. heseloni*). The pits for the collateral ligaments are located close to the mid-line so that the articular surface is pinched dorsoproximally. On the plantar side, the articular surface is more extensive proximally near the medial and lateral sides, which accommodate the sesamoid bones. However, “fluting” to separate sesamoid areas from the central part (Lewis, 1989) is absent. This suggests that the metatarsophalangeal joint allowed higher degrees of abduction-adduction and rotations, though not as extensively as is in extant great apes (Rose et al., 1996). The shaft is circular in cross section and thicker than the distal shaft of KNM-BG 35250AM (6.2 mm d-p and 6.1 mm m-l at the break).

Discussion

The hind limb of *N. kerioi* is generally similar to those of other early/middle Miocene African hominoids but shows some distinctive traits. However, the distinctiveness is less outstanding when compared to its forelimb. This is probably due to differentiated functional roles in positional behavior between the fore- and

hind limbs of primates. While the forelimb determines the direction of movement and the body position with respect to support, the hind limb principally works to produce propulsive force. Therefore, without some specialized form of locomotor/positional adaptation (e.g., leaping, running, deep crouching), the hind limb may retain generalized ancestral morphology. The hind limb of the early Oligocene *Aegyptopithecus* was primarily adapted for arboreal pronograde quadrupedalism and (to a lesser degree) climbing (Ankel-Simons et al., 1998) with some leaping (Gebo and Simons, 1987). The early Miocene *Proconsul* had limb bones reminiscent of such ancestral catarrhine condition except a few major differences such as more elongated limb long bones and wider excursions of the limb joints (Walker, 1997). Probably, *Proconsul* was a predominantly arboreal and slow-moving quadruped relying on strong grasping. This condition is largely retained in the hind limb of *N. kerioi*. Rose (1983) has rightly noted this point as follows: “differences between earlier and later Miocene hominoids are mostly of degree rather than of kind. The basic plan upon which these variations were made was evidently a very successful one. This success was based on a generalized morphology underlying generalized capabilities (P. 415).”

The present study corroborated the initial interpretation of the hind limb anatomy of *N. kerioi* (Rose et al., 1996). *N. kerioi* has an extremely developed capacity for foot grasping. Rose et al. (1996) correlated the development of the medial process of the plantar calcaneal tuberosity (Figure 9d) with the development of the intrinsic toe flexors, which can work without being interrupted by movement/posture of the ankle joint. Morphology of the hallucal MT head led Rose et al. (1996) to conclude that abduction-adduction and axial rotations (for hallucal grasping) are as important as flexion-extension at the MT-phalangeal joint. One of the most remarkable specializations in *N. kerioi* is its absolutely large foot. The distal portion of the foot is as long as that of *P. nyanzae* whose body mass could reach as much as 35 kg (Rafferty et al., 1995) or 1.5 times that of *N. kerioi*. The (non-hallucal) MTs appear relatively gracile due to elongation whereas the proximal joints are enlarged. Although the distal tarsal row is represented only by the medial cuneiform, which is large for the

presumed body mass, other cuneiforms and cuboids are probably large at least in their distal portions. Likewise, the length of the hallux is comparable to that of female chimpanzees (Nakatsukasa et al., 2003). A large foot with a developed hallux likely enabled *N. keroi* to grasp relatively thick vertical supports securely. This suggests a more frequent use of (sub)vertical supports compared to above-branch pronograde quadrupeds like *Proconsul* though this does not mean *Proconsul* did not rely on hallucal grasping while moving on branches.

The inferred kinetic features of the talocrural and intertarsal joints are similar to those of the other fossil hominoids regarding the range of movements and magnitude of stability, and in these regards, early/middle Miocene African hominoids are intermediate between cercopithecids and extant great apes, and more similar to the former (Conroy and Rose, 1983; Walker and Pickford, 1983; Langdon, 1986; Rose, 1993; Ward et al., 1993). The ankle joint assumed the close-packed position in full dorsiflexion similar to cercopithecids. The talocrural and subtalar joints do not have extra inversion and enhanced conjunct inversion and abduction accompanying dorsiflexion as seen in extant great apes. However, the foot of *N. keroi* might have been more specialized to take an inverted position to grasp (sub)vertical support if compared with *Proconsul* or *A. turkanensis*. This is suggested from the thick tibial malleolus and the emphasized elevation of the lateral rim of the talar trochlea.

Adaptation of the hip and knee joints is somewhat vague. Rose et al. (1996) noted that *N. keroi* differ from *Proconsul* in several hind limb traits; a shorter neck, more medially directed lesser trochanter, a shorter distance between the gluteal tuberosity and greater trochanter, more gracile proximal shaft of the femur, partial external rotation with the knee semi-flexed and pointing laterally. However, the morphology of the knee seems to preclude habitual abduction (combined with flexion). *N. keroi* might have adopted varying (atypical) knee positions rather than general habitual knee abduction. The *Proconsul* hip joint probably allowed the species to take a wide variety of postures/movements (Ward et al., 1993). However, it might have also taken strongly

abducted positions more frequently. The same inference has been put forth for *Sivapithecus* (Madar et al., 2002). Probably, the hip and knee joints in these fossil apes were not specialized for any single particular behavior, but relative frequencies of various joint motions/postures. Therefore, functional meanings that account for noticeable morphological variability are difficult to specify. More specimens are needed to reach any explicit conclusion.

In summary, the hind limb of *N. kerioi* shows a greater affinity to other hominoids from the early/middle Miocene of Africa (e.g., *Proconsul*, *Afropithecus*, *Equatorius*) than to extant hominoids. However, several characters that distinguish *N. kerioi* from other early/middle Miocene African hominoids do exist. These features are suggestive of a greater role of antipronograde activities in *N. kerioi* compared to other Miocene “pronograde arboreal quadrupeds”.

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Figure legends

Figure 1

Ischia of *N. kerioi*. a: left (KNM-BG 35250G). b: right (KNM-BG 35250Y). Note a large ischial spine located relatively cranially. Scale bar = 1 cm.

Figure 2

Right proximal femur (KNM-BG 35250A) in proximal (a), anterior (b) and posterior view (d) and left proximal femur (KNM-BG 35250D) in anterior (c) and posterior view (e). The head of KNM-BG 35250A is anteriorly displaced and rotated anteromedially. The latter is postmortem deformation. Note the wide articular cover of the head (arrow in (d) indicates the articular margin). Horizontal lines in (d) and (e) shows the relative elevation of the greater trochanter. In (e) arrows indicate the large crista trochanterica. Scale bar = 5 cm.

Figure 3

Left distal femur (KNM-BG 35250J) in anterior (a) and posterior view (b) and right distal femur (KNM-BG 35250B) in medial (c) and lateral view (d). Note a square-shaped patellar surface (shown by arrows in (a)) and condylar width symmetry (compare white lines in (b)). In *P. nyanzae* (KNM-RU5527 left femur), the patellar surface is trapezoidal with a more raised lateral rim and the medial condyle is asymmetrically wider than the lateral one (e). lc: fovea for the lateral collateral ligament. po: depression for the tendon of *m. popliteus*. mc: fovea for the medial collateral ligament. Scale bar = 5 cm.

Figure 4

Proximal fragment of the right patella (KNM-BG 35250Z) in proximal (a), anterior (b) and posterior view (c).

Scale bar = 1 cm.

Figure 5

Tibiae of *N. kerioi* and *P. nyanzae* a: Left tibia fragments (KNM-BG 35250E/AF/H) in lateral view. b-c: Left proximal tibia (KNM-BG 35250E) in medial (b) and proximal (c) view. d-f: right distal tibia (KNM-BG 35250L) in distal (d), lateral (e), and posterior (f) view. g: left distal tibia in distal view (KNM-BG 35250H). h: right proximal tibia (KNM-BG 35250AE) in lateral view. i-j: Left tibia of *P. nyanzae* (KNM-RU 1939) in lateral (i) and posterior (j) view. Note the thick medial malleolus of *N. kerioi* (d, f). Scale bar = 5 cm.

Figure 6

Fibulae of KNM-BG 35250. Left shaft KNM-BG 35250AH in anterior (a) and medial (b) view. c: left distal fragment KNM-BG 35250F in medial view. Right shaft KNM-BG 35250AG in anterior (e) and medial (d) view. f: right distal fragment KNM-BG 35250K. Scale bar = 2 cm.

Figure 7

Left talus of *N. kerioi* KNM-BG 35250I in dorsal (a), plantar (b), lateral (c), medial (d) and distal (e) view. st: *sulcus tali*. tn: attachment of talonavicular ligament. Scale bar = 1 cm.

Figure 8

Tali of fossil hominoids in posterior view. a: *N. kerioi* KNM-BG 35250I. b: *N. kerioi* KNM-BG 15529 (reversed). c: *P. nyanzae* KNM-MW 13142C (reversed). d: *P. nyanzae* KNM-RU 1743. e: *A. turkanensis* KNM-WK 18120. f: *U. major* KNM-SO 390 (reversed). Photographs were taken with the lateral side of the

trochlea being set vertical. White lines compare the orientation of the trochlear surface. Not to scale.

Figure 9

Right calcanei of *N. kerioi*. a-c: KNM-BG 35250O in dorsal (a), medial (b) and distal (c) view. d-e: KNM-BG 17805 in medial (d) and dorsal (e) view. f: KNM-BG 15532 in dorsal view. The arrow indicates the most distal part of the medial process of the plantar calcaneal tuberosity. Scale bar = 1 cm.

Figure 10

a-d: Fossil left medial cuneiforms. *N. kerioi* KNM-BG 35250AI in medial (b), distal (b) and lateral (c) view. *P. nyanzae* KNM-RU 5872G in medial view (d). Scale bar = 1 cm. f: articulated medial cuneiform and hallucal metatarsal of *P. nyanzae* KNM-RU 5872. Note the articular areas for the prehallux (arrows).

Figure 11

a-c: right hallucal metatarsal of *N. kerioi* (KNM-BG 35250AJ) in medial (a), lateral (b), proximal (c) view. d: left hallucal metatarsal of *P. nyanzae* (KNM-RU 5872E) showing the prehallux facet (asterisk). For convenience, orientations are defined by the human standard anatomy (not in the opposed position). Dorsal surface upward. e, f: left second metatarsal (KNM-BG 35250AK) in proximal (e) and dorsal (f) view. g, h: left fourth metatarsal (KNM-BG 35250AL) in proximal (g) and dorsal (h) view. i, j: distal fragment of metatarsal in dorsal (i) and distal (j) view. k-m: left fifth metatarsal of *N. kerioi* (KNM-BG 35250AM) in dorsal (k) and plantar (l) view and of *P. nyanzae* (KNM-RU 5872H) in dorsal view (m). Arrow indicates the origin of *m. flexor digiti minimi brevis*. Scale bar = 1 cm.

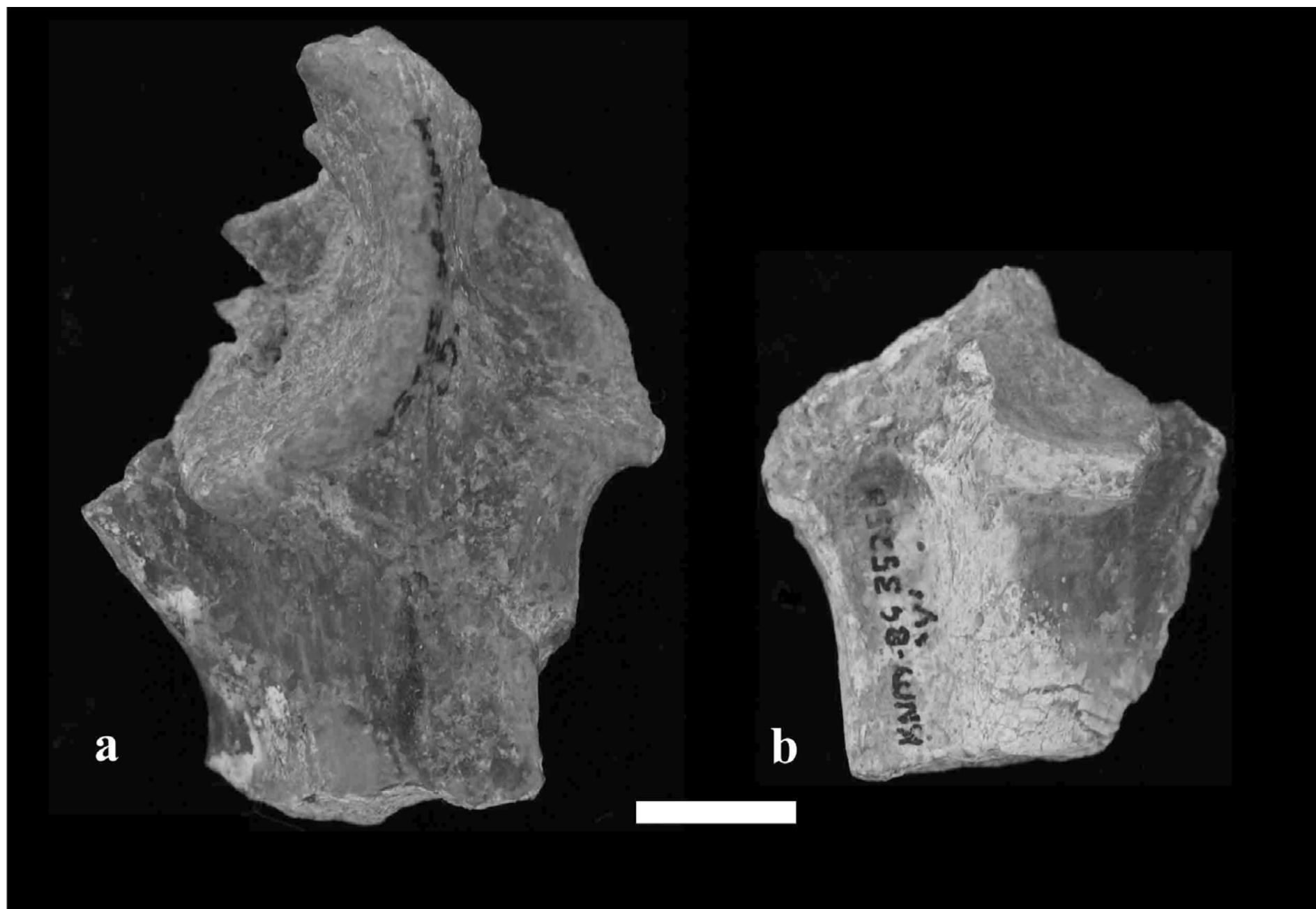


Figure 1



Figure 2



Figure 3

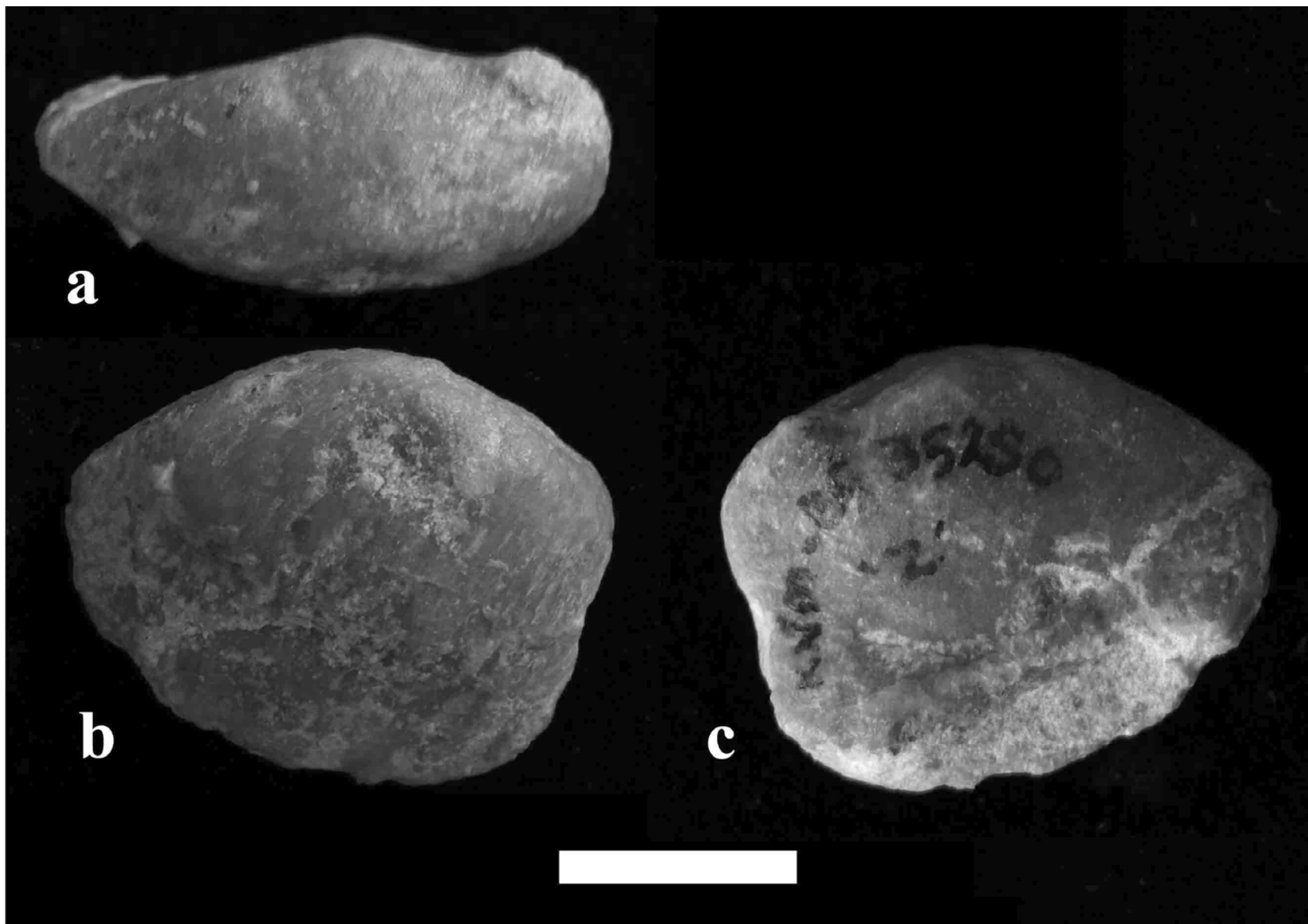


Figure 4

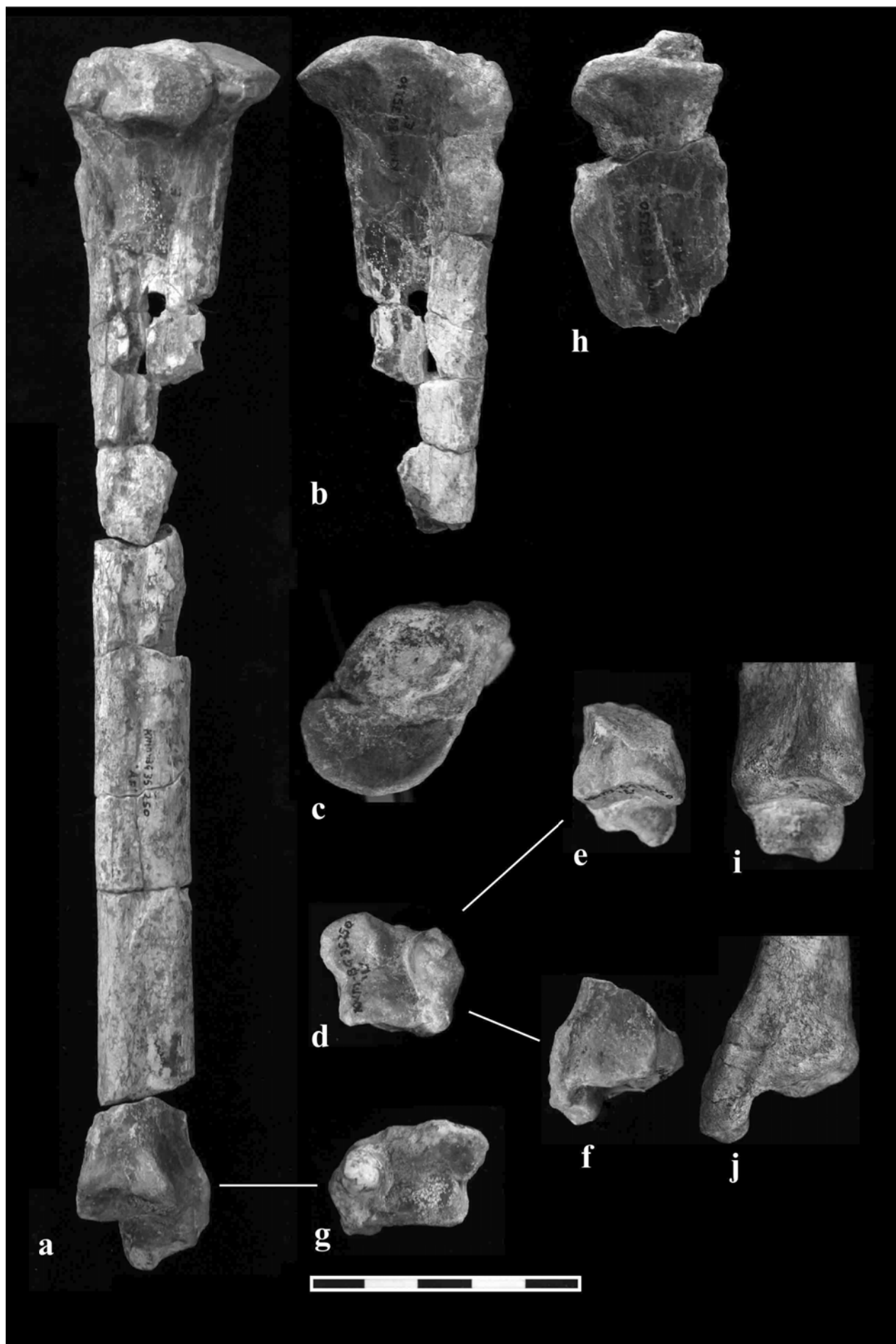


Figure 5

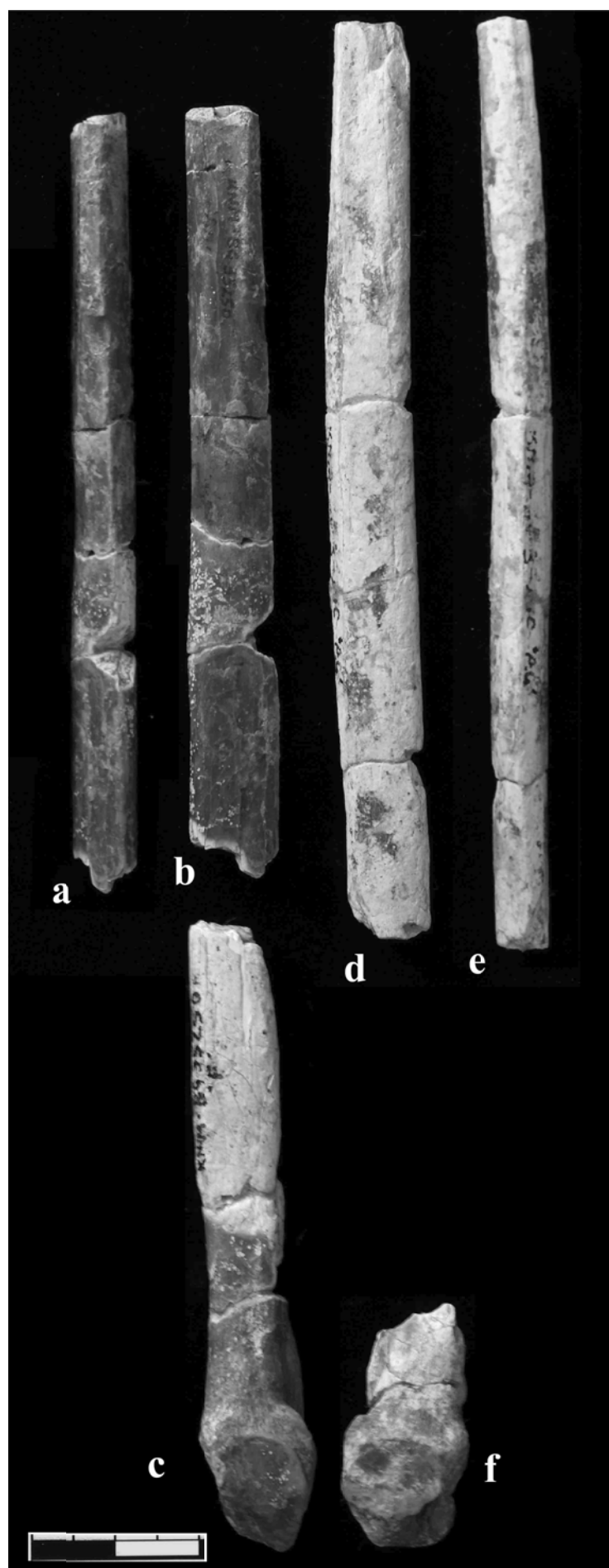


Figure 6

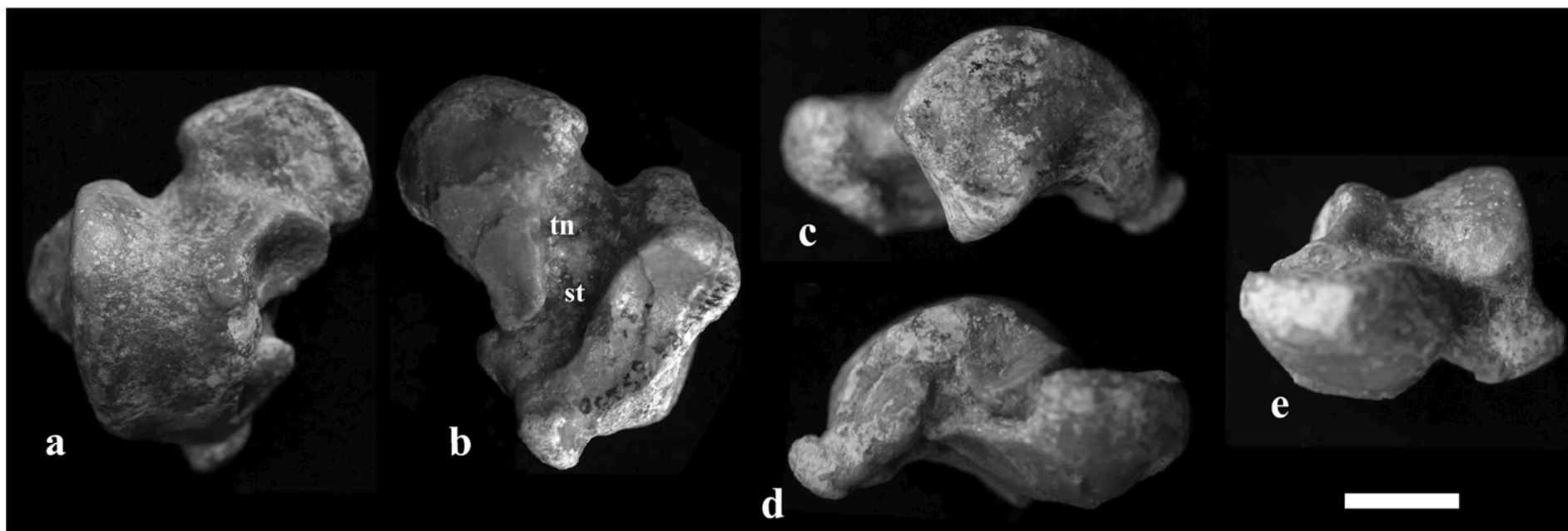


Figure 7

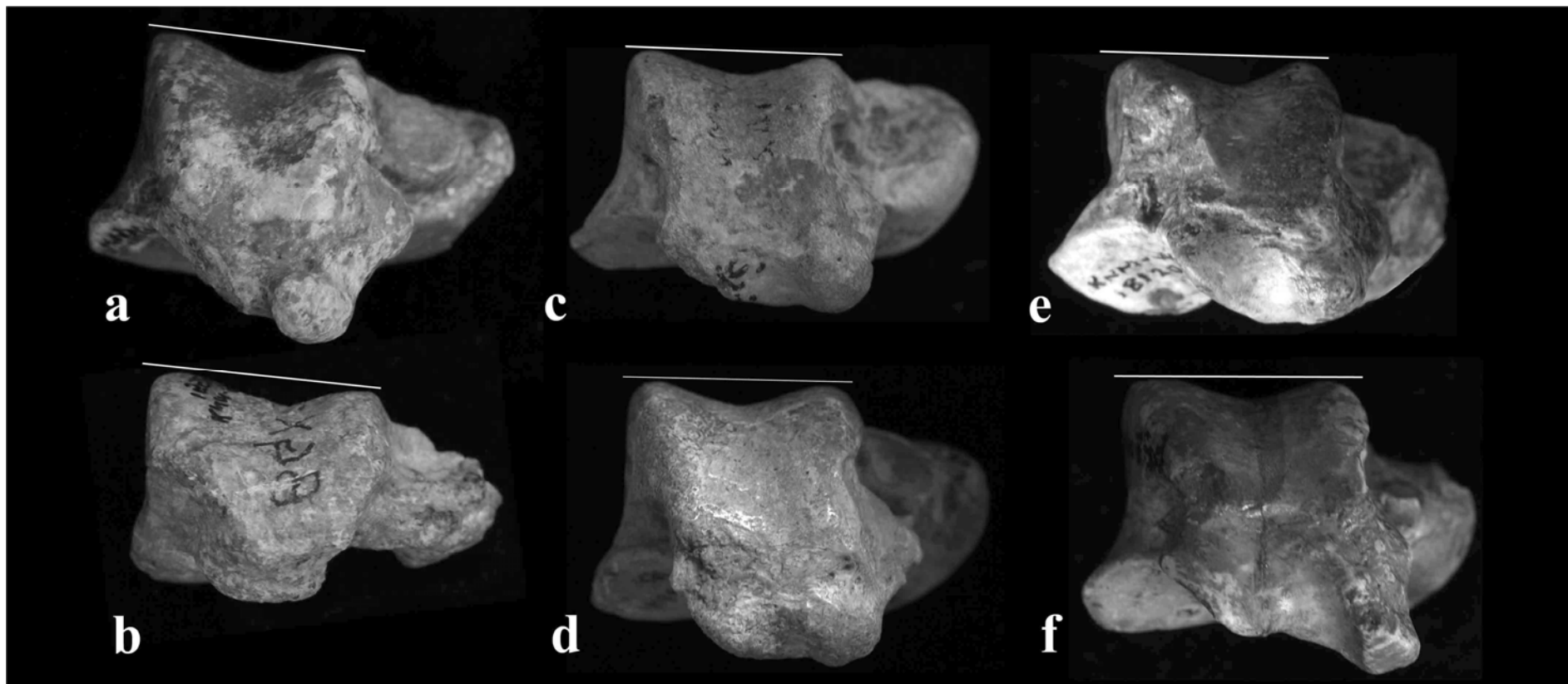


Figure 8

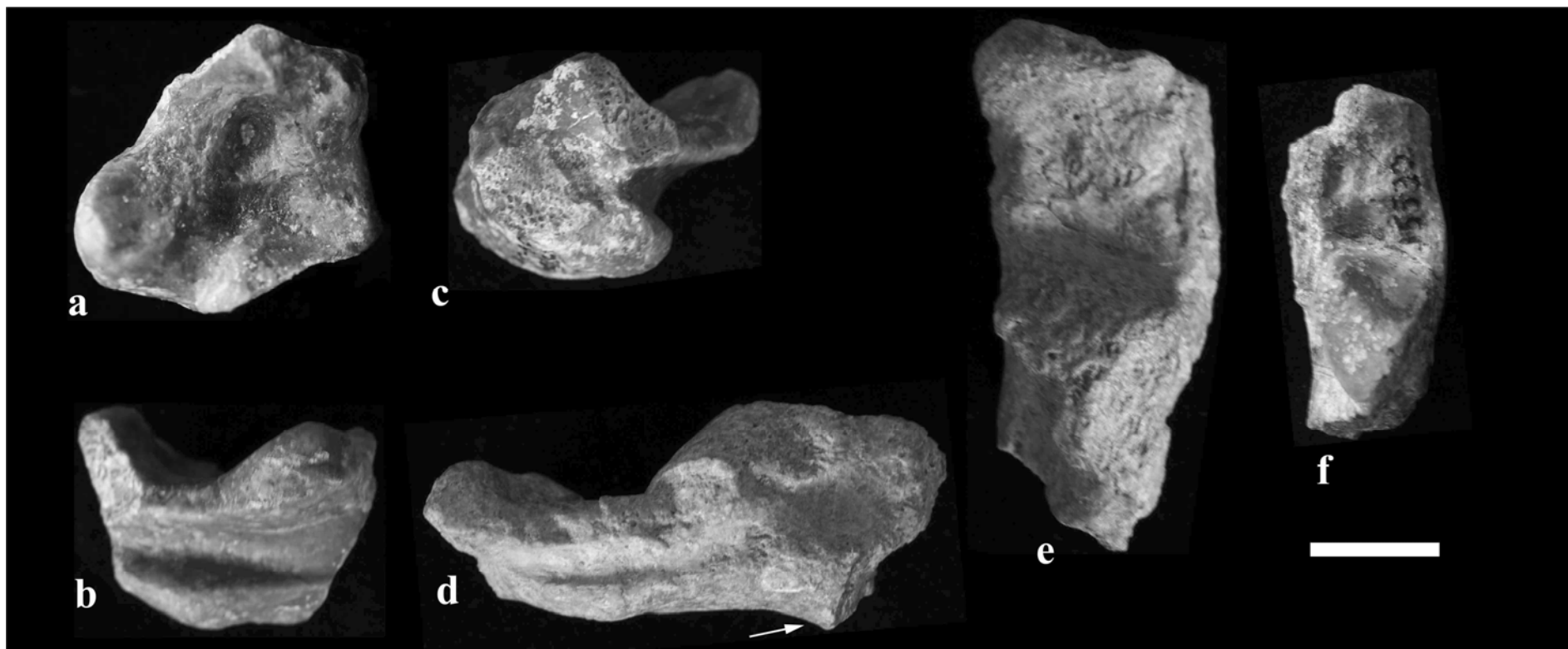


Figure 9

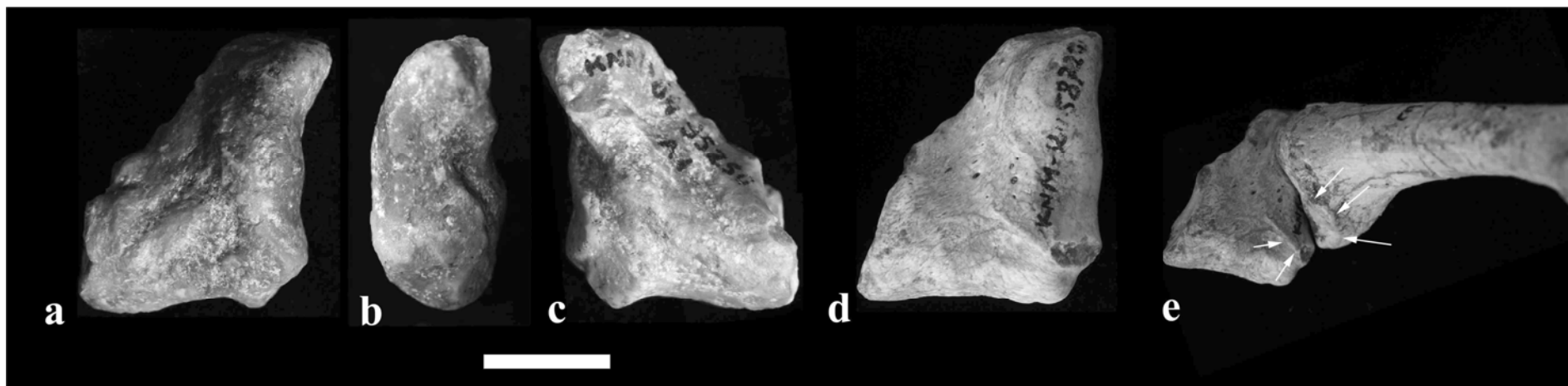


Figure 10



Figure 11

Table 1 Hind limb elements of KNM-BG 35250 described in this study.

suffix	description
A	right proximal 1/2 femur
B	right distal 1/3 femur
D	left proximal femur
E	left proximal 1/3 tibia
F	left distal fibula
G	left ischium
H	left distal tibia
I	left talus
J	left femoral shaft and distal end
K	right distal fibula
L	right distal tibia
O	right calcaneus
Y	right ischium
Z	right patella proximal fragment
AE	right proximal tibia
AF	left tibial shaft
AG	right fibula shaft
AH	left fibula shaft
AI	left medial cuneiform
AJ	right first metatarsal proximal half
AK	left second metatarsal proximal fragment
AL	left fourth metatarsal proximal fragment
AM	left fifth metatarsal lacking the head
AN	metatarsal head with shaft

Table 2 Metric comparison of the femur.

taxon		sex	SIFD	%SIFD	GTPR	%APFN	%LCW
<i>Nacholapithecus</i>	KNM-BG 35250A & D	m	22.1	159.8	-1.5	72.8	98.8
<i>Nacholapithecus</i>	KNM-BG 17821	m	-	-	-	77.5	-
<i>Nacholapithecus</i>	KNM-BG 17778	f	17.6	-	-	-	-
<i>Proconsul nyanzae</i>	KNM-MW 13142A	m	28.7	166.2	-1.0	78.5	-
<i>Proconsul nyanzae</i>	KNM-RU 5950	m	25.3	157.9	-	77.5	-
<i>Proconsul nyanzae</i>	KNM-RU 5527	?m	25.5	158.3	-	73.4	76.6
<i>Proconsul nyanzae</i>	KNM-RU 1753	m	26.7	-	-	-	-
<i>Proconsul heseloni</i>	KNM-RU 14227	f	-	-	-	-	89.6
<i>Proconsul heseloni</i>	KNM-KPS 3 (right)	f	16.7	-	-	-	-
<i>Proconsul</i>	Mean		-	160.8	-	76.5	83.1
<i>Equatorius</i>	BM-M16331	?m	22.8	164.4	-	76.1	-
<i>Morotopithecus</i>	MUZM 80	?	26.5	139.8	-1.5	88.1	81.1
<i>Ugandapithecus</i>	NAP IX B'64/65	m	30.9	152.3	-4.0	77.8	-
<i>Turkanapithecus</i>	KNM-WK 16950I	?m	17.6	149.7	-1.2	78.2	-
<i>Pan troglodytes</i>	Mean	f	31.14	169.73	-2.44	85.29	81.14
9 females	SD		1.84	12.34	2.99	5.42	4.18
<i>Pongo pygmaeus</i>	Mean	f	31.50	182.51	-13.50	73.60	90.85
4 females	SD		1.07	13.06	1.73	4.59	4.78
<i>Hyobates lar</i>	Mean	m	16.30	191.94	-1.75	82.11	75.67
10 males	SD		0.58	7.27	1.18	4.81	4.59
<i>Papio cynocephalus</i>	Mean	m	23.36	151.85	9.20	73.97	88.20
10 males	SD		1.06	9.30	1.55	2.47	4.87

SIFD: s-i diameter of the femoral head. %SIFD: relative head size (= SIFD / (neck s-i diam. x a-p diam.)^{0.5} x 100). GTPR: greater trochanter projection relative to the head superior surface. %APFN: relative a-p diam. of the neck (= a-p diam. of the neck / s-i diam. x 100). %LCW: relative width of the lateral condyle (= lateral condyle w. / medial condyle w. x 100).

Table 3 Size and shape of the tibial malleolus. For extant taxa, average (upper) and SD (lower).

taxon	Height (mm)	Width (mm)	width/height (%)
<i>Nacholapithecus kerioi</i> KNM-BG 35250L	9.7	9.3	95.88
<i>Proconsul heseloni</i> N = 4	7.83 0.51	6.33 0.13	81.14 6.38
<i>Proconsul nyanzae</i> KNM-RU 1939	12	9.5	79.17
<i>Ugandapithecus major</i> NAP I 1958	13.1	13.8	105.34
<i>Pan troglodytes</i> 8 females	13.06 1.62	12.61 0.56	97.75 11.72
<i>Pongo pygmaeus</i> 4 females	8.5 1.8	11.53 0.38	138.96 21.39
<i>Hylobates lar</i> 10 males	6.38 0.54	6.01 0.38	94.56 6.90
<i>Papio cynocephalus</i> 10 males	11.27 0.63	8.73 0.62	77.46 3.67

Proconsul heseloni: KNM-RU 2036BA, 3589, 18390, KPS 3 (TB6).